



THE PALAEOBIOGEOGRAPHY OF MESOZOIC MAMMALS: A REVIEW ¹

(With 21 figures)

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ABSTRACT: The fossil record of Mesozoic mammals is much more meagre than that of Cainozoic ones. Despite this deficiency, it is possible to make some useful generalisations about the biogeographic history of this group during the Mesozoic Era. Compared with the Jurassic, where cosmopolitanism is frequent amongst the various mammalian families, regionalism is more commonly the case in the Cretaceous, particularly the Late Cretaceous. This reflects the progressive breakup of first Pangea and then Gondwana as the Mesozoic Era progressed. The conventional hypothesis that the therians arose on the northern continents and spread to the southern ones owes much of its strength to the poor Mesozoic mammalian record in the latter. Recent discoveries in the Southern Hemisphere suggest that caution is warranted in accepting the conventional hypothesis.

Key words: Palaeobiogeography. Fossil mammals. Mesozoic.

RESUMO: Paleobiogeografia dos mamíferos mesozóicos: uma revisão.

O registro fóssil de mamíferos do Mesozóico é bem mais escasso que o do Cenozóico. Apesar dessa deficiência, é possível fazer algumas generalizações sobre a história bioestratigráfica desse grupo durante a Era Mesozóica. Comparado com o Jurássico, onde o cosmopolitismo é freqüente entre as várias famílias de mamíferos, o regionalismo é mais comum no Cretáceo, particularmente no Cretáceo Superior. Isto reflete a separação progressiva do Pangea e do Gondwana, à medida que a Era Mesozóica progredia. A hipótese convencional de que os Theria se originaram dos continentes do norte e se dispersaram para os do sul se deve ao pobre registro de mamíferos do Mesozóico nestes últimos. Descobertas recentes no Hemisfério Sul sugerem que é necessário se ter maior cautela para se aceitar a hipótese convencional.

Palavras-chave: Palaeobiogeografia. Mamíferos fósseis. Mesozóico.

INTRODUCTION

In 1947, George Gaylord Simpson published a detailed analysis of the distribution of mammals in North America and Eurasia during the Cainozoic (SIMPSON, 1947) (Fig.1). In this paper, he pioneered quantitative methods for assessing the interchange between the two areas. This paper stands as a model of how mammalian biogeography should be done.

Ideally, Simpson's methodology should be extended into the Mesozoic. However, several factors make that impractical. In the first place, there are far fewer mammalian taxa in the Mesozoic than the Cainozoic. Were Simpson writing that paper today on a worldwide scale, in the Cainozoic there would be about 3,500 non-volant terrestrial mammalian genera available for analysis. This is in stark contrast to the 300 mammalian genera known from the Mesozoic. For the Cainozoic, there are 50 genera for every one

million years while for the Mesozoic, only two.

Second, the Mesozoic mammalian fossil record is much more incomplete than the Cainozoic. There are large temporal gaps in the Mesozoic record (Fig.2) and the number of sites where Mesozoic mammals occur is quite uneven (Fig.3). North America in the Late Cretaceous, for example, has a number of sites comparable to the Palaeocene on that continent while Australia has only four sites in the late Early Cretaceous and none in all other parts of the Mesozoic. Generally, the Gondwanan continents have far fewer sites than Laurasia, making the recognition of biogeographic phenomena in the former quite tentative for the most part.

METHODS

Unless otherwise specified, the distribution data for Mesozoic mammals given in this paper is taken from KIELAN-JAWOROWSKA *et al.* (2004).

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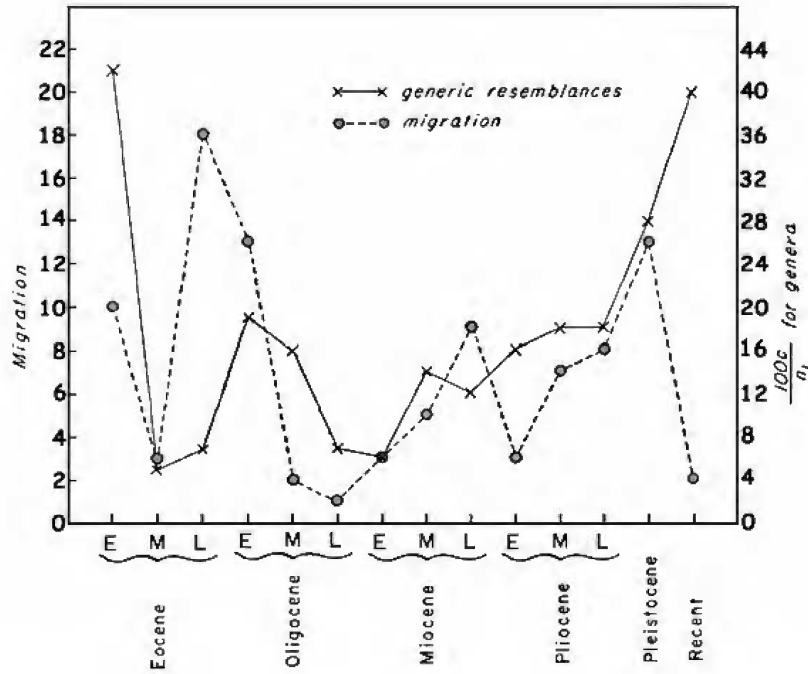


Fig.1- Figure 4 in SIMPSON (1947). Number of genera in common between North America and Eurasia during the Cainozoic (solid line) and amount of migration (dashed line) between the two land masses. From SIMPSON (1947).

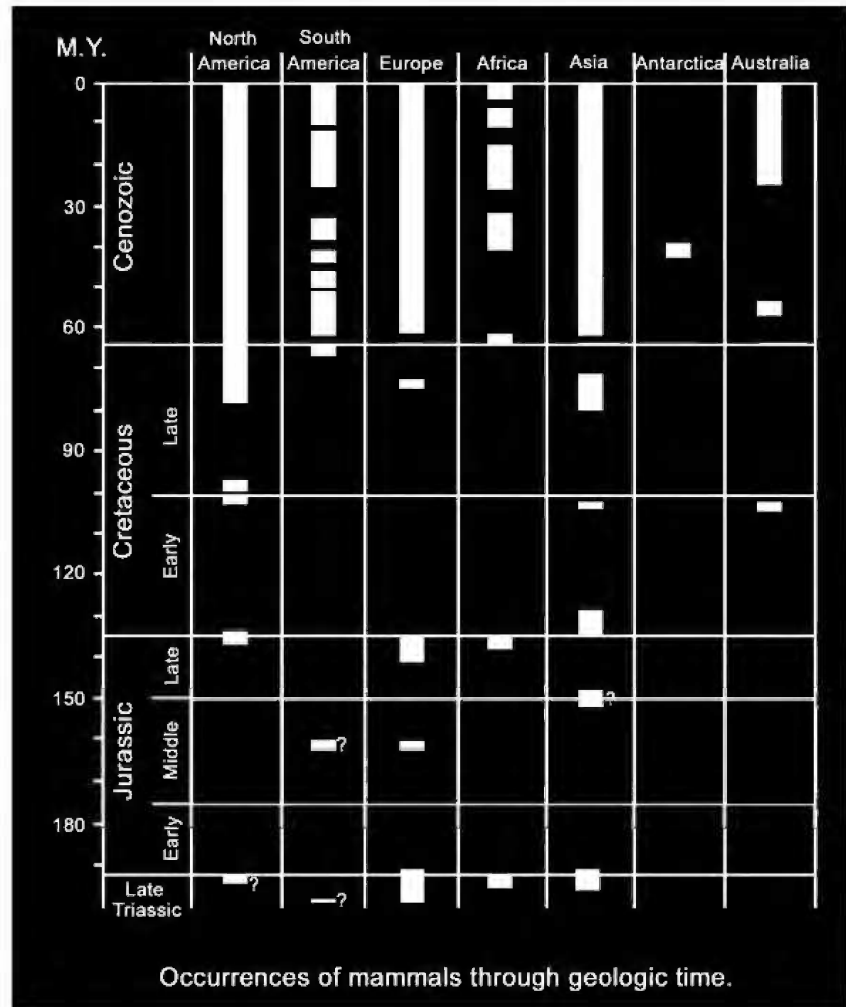


Fig.2- Periods of time in the Mesozoic and Cainozoic when fossil mammals are known on the various land masses (modified from LILLEGRAVEN *et al.*, 1979).

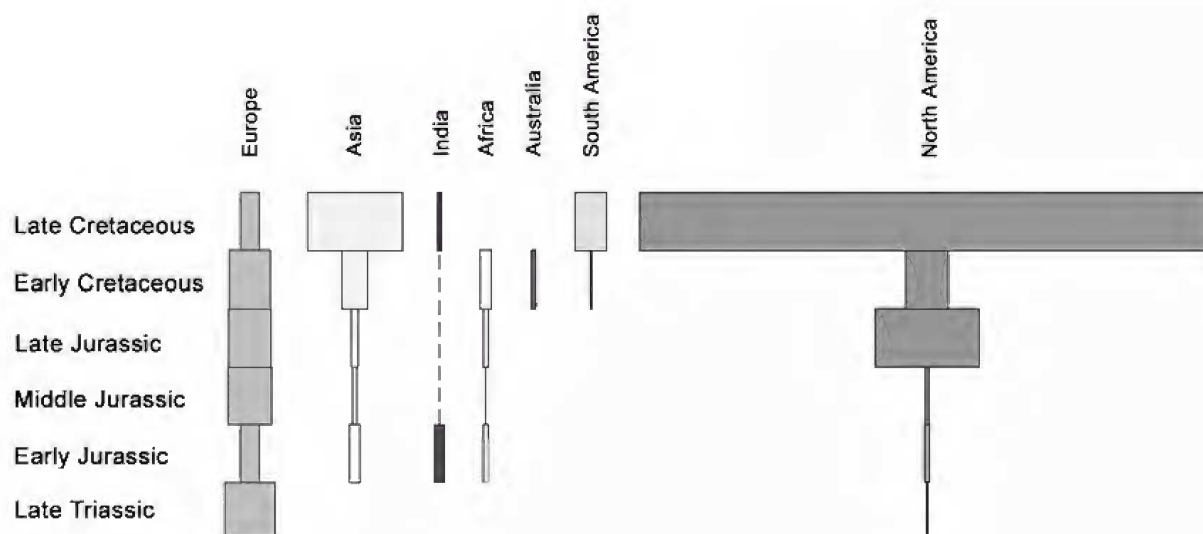


Fig.3- Relative numbers of Mesozoic mammals by continents and age. "For most pre-Late Cretaceous occurrences and virtually all occurrences outside of North America, the totals reflect all taxa from all known sites and in many cases reflect most known individual specimens. Lumping occurrences by local faunas results in under representation for the North American Late Cretaceous, which nonetheless includes a disproportionately large number of occurrences" (KIELAN-JAWOROWSKA *et al.*, 2004, p.108).

DISCUSSION

The depth of our ignorance about the distribution of Mesozoic mammals is well illustrated by the multituberculates. A distribution map of them drawn in 1980 would show the group confined to the Laurasian continents where their remains were quite abundant (Fig.4). At that time, it was quite reasonable to envision them as an exclusively Laurasian group. In the twenty-five years that have passed, records of them, some of them tentative, have been found in Africa and South America (Fig.5). These Gondwanan records are based on a handful of specimens. With this paucity of Gondwanan material, can we safely conclude that the multituberculates were primarily a Laurasian group with a few species in Gondwana? Given the few specimens of mammals of any kind that occur where these Gondwanan Mesozoic multituberculates have been found, that is an interpretation of the evidence that seems unwarranted. True, they are rare as fossils but as part of living communities, they may have been quite abundant. We simply cannot tell from the available specimens.

The Mesozoic palaeobiogeography of mammals can conveniently be divided into the Late Cretaceous and the pre-Late Cretaceous. This is owing to two factors. First, during the Late Cretaceous the number of productive fossil mammal sites and hence the record

is much better. Second, the extant metatherians and eutherians are a significant part of the Late Cretaceous mammalian assemblage and hence molecular techniques can be applied to their living descendants to get additional insights about them.

The Morganucodontidae are either regarded as amongst the most primitive mammals or mammaliformes close to the base of the Mammalia. Because of this, they provide a clue as to the place of origin of the Mammalia. In the late Triassic, except for Greenland, they occur on every landmass where any mammals or mammaliforms are known (Fig.6). From this, in the highly appropriate words of Jason Lillegraven in another context, the conclusion seems to be that mammals arose somewhere on the Earth's dry surface.

Because in the Mesozoic, there is only about 4% as much data concerning mammalian distributions per unit time as is available in the Cainozoic, only the broadest biogeographic generalisations are possible. Despite this drawback, a significant contrast can be seen in the distribution of mammalian families in the Jurassic as opposed to the Cretaceous (Figs.7-8). A greater percentage of the Jurassic families occur on two or more land masses than is the case in the Cretaceous. This is concordant with the closer proximity of the land masses during the Jurassic as compared with the Cretaceous when the break up of Pangea had proceeded much further.

Known Distribution of the Multituberculates 1980



Fig.4- Land masses where multituberculates were known to have been present in 1980.

Known Distribution of the Multituberculates 2005



Fig.5- Land masses where multituberculates were known to have been present in 2005.

Interestingly, in the both the Jurassic and Cretaceous, there are more links between individual Gondwanan land masses and Laurasian ones than there are between pairs of Gondwanan land masses. This is presumably due to the fact that many more families are known on the Laurasian land masses so, all else being equal; a match is more likely to be found there. Given the continental positions, particularly in the Jurassic, it seems unlikely that these greater frequencies of connections of the Gondwana land masses with those to the north rather than to each other was actually the case.

What this broad brushstroke data cannot do is to provide evidence for the direction of movement between land masses. That would require far more information, particularly well dated sites.

Unquestioned docodontids are known only from Laurasia and range in age from Middle Jurassic to Early Cretaceous. Outside of this temporal and geographic range, there are two specimens that may be docodonts. First is a single Late Triassic tooth from France assigned to the genus *Delsatia* (SIGOGNEAU-RUSSELL & GODEFROIT, 1997).

Distribution of the Morganuodontidae

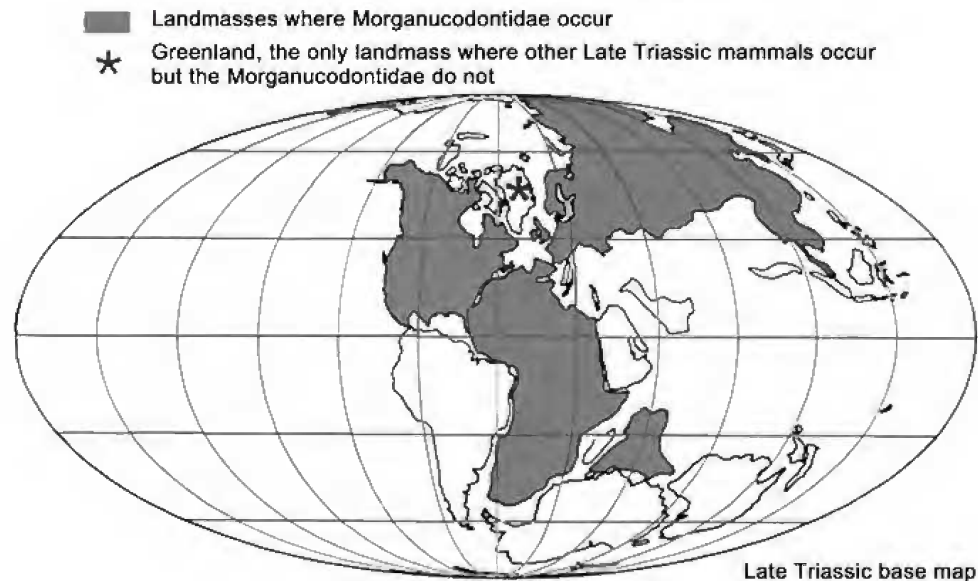


Fig.6- Known distribution of the Morganuodontidae. Base map Late Triassic.

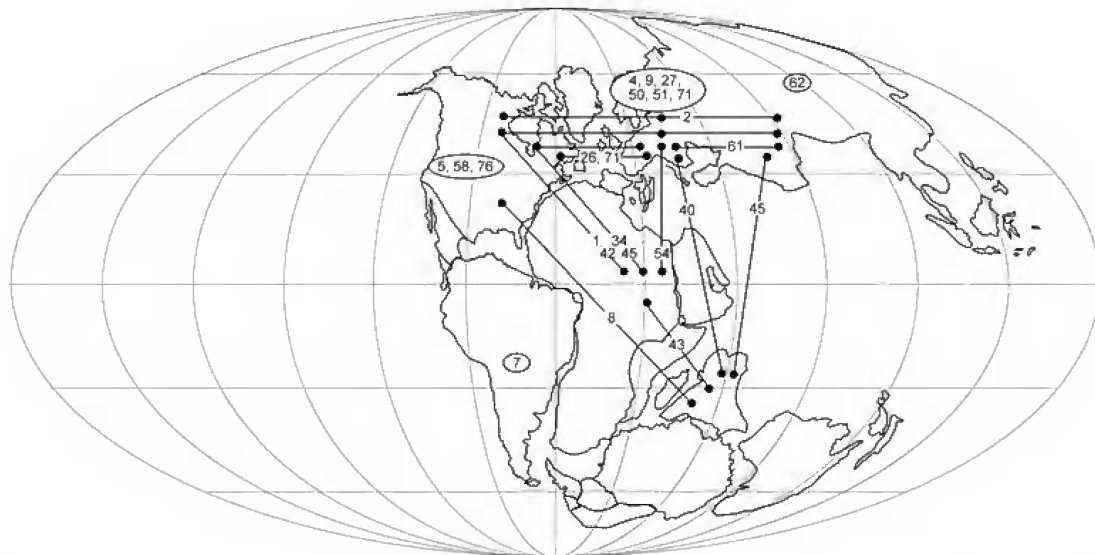


Fig.7- Records of Jurassic mammalian families on a Bajocian basemap. The same families found on two or more landmasses are linked together by a solid line. The linkage lines do not necessarily imply migration routes or directions of separation of land masses in vicariant events. For example, the Morganuodontidae are known both in India and Asia. The line linking them passes through Europe, North America, and Africa. Despite this, the interchange between Asia and India could have been more direct. 1. "Amphilestidae"; 2. Aegialodontidae; 3. Aguitheriidae; 4. Albionbaataridae; 5. Allodontidae; 6. Alphadontidae; 7. Ameghinichnidae; 8. Amphidontidae; 9. Amphitheriidae; 10. Arctocyonidae; 11. Arginbaataridae; 12. Arguimuridae; 13. Asiatheriidae; 14. Asioryctidae; 15. Ausktribosphenidae; 16. Austrotriconodontidae; 17. Barbereniidae; 18. Bobolestidae; 19. Bondesiidae; 20. Cimolodontidae; 21. Cimolomyidae; 22. Deltatheridiidae; 23. Djadochtatheriidae; 24. Docodontidae; 25. Donodontidae; 26. Dryolestidae; 27. Eleutherodontidae; 28. Eobaataridae; 29. Eucosmodontidae; 30. Ferugliotheridae; 31. Glasbiidae; 32. Gobiconodontidae; 33. Hahnodontidae; 34. Haramiyidae; 35. Hyopsodontidae?; 36. Kennalestidae; 37. Kermackiidae; 38. Kogiaononidae; 39. Kollikodontidae; 40. Kuehneotheriidae; 41. Kulbeckiidae; 42. Leptictidae; 43. Megazostrodonidae; 44. Mesungulatidae; 45. Morganuodontidae; 46. Neoplagauiacidae; 47. Nyctitheriidae; 48. Otlestidae; 49. Palaeoryctidae; 50. Pappotheriidae; 50½ Paulchoffatiidae; 51. Paurodontidae; 52. Pediomysidae; 53. Peradectidae?; 54. Peramuridae; 55. Periptychidae; 56. Picopsidae; 57. Pinheiroodontidae; 58. Plagauiacidae; 59. Ptilodontidae; 60. Reigitheriidae; 61. Shuotheriidae; 62. Sinoconodontidae; 63. Sloanbaataridae; 64. Spalacotheriidae; 65. Stagodontidae; 66. Steropodontidae; 67. Sudamericidae; 68. Taeniolabididae; 69. Thereuodontidae; 70. Theroteinidae; 71. Tinodontidae; 72. Triconodontidae; 73. Vincelestidae; 74. Zalambdalestidae; 75. Zhelestidae; 76. Zofiabaataridae.

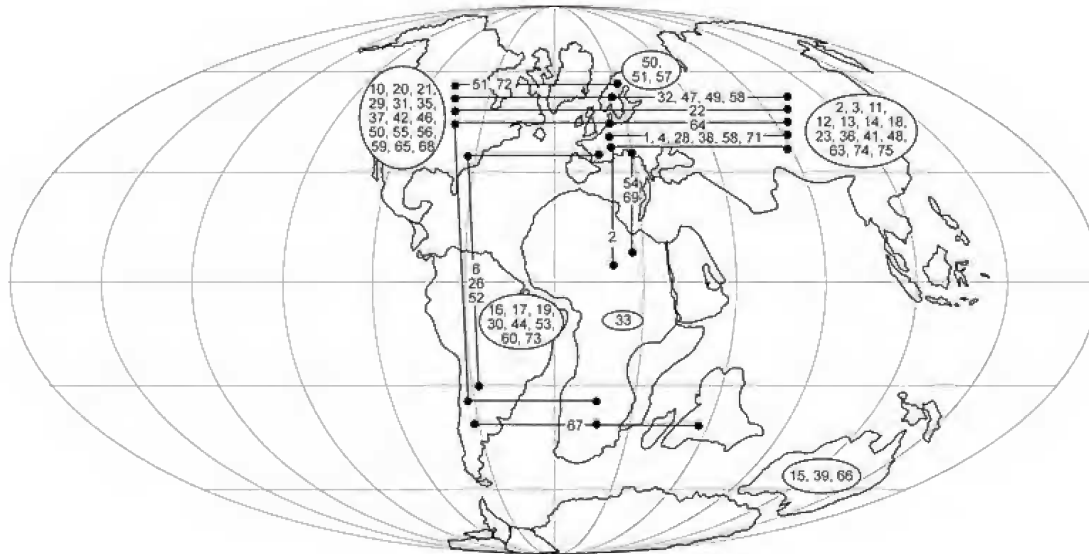


Fig.8- Records of Cretaceous mammalian families on an Albian basemap. For explanation, see caption for figure 7. 1. "Amphilestidae"; 2. Aegialodontidae; 3. Aguitheriidae; 4. Albionbaataridae; 5. Allodontidae; 6. Alphadontidae; 7. Ameghinichnidae; 8. Amphidontidae; 9. Amphitheriidae; 10. Arctocyonidae; 11. Arginbaataridae; 12. Arguimuridae; 13. Asiatheriidae; 14. Asioryctidae; 15. Ausktribosphenidae; 16. Austroconodontidae; 17. Barbereniidae; 18. Bobolestidae; 19. Bondesiidae; 20. Cimolodontidae; 21. Cimolomyidae; 22. Deltatheridiidae; 23. Djadochtatheriidae; 24. Docodontidae; 25. Donodontidae; 26. Dryolestidae; 27. Eleutherodontidae; 28. Eobaataridae; 29. Eucosmodontidae; 30. Ferugliotheridae; 31. Glasbiidae; 32. Gobiconodontidae; 33. Hahnodontidae; 34. Haramiyidae; 35. Hyopsodontidae?; 36. Kennalestidae; 37. Kermackiidae; 38. Kogiaononidae; 39. Kollikodontidae; 40. Kuehneotheriidae; 41. Kulbeckiidae; 42. Leptictidae; 43. Megazostrodonidae; 44. Mesungulatidae; 45. Morganucodontidae; 46. Neoplagiaulacidae; 47. Nyctitheriidae; 48. Otlestidae; 49. Palaeoryctidae; 50. Pappotheriidae; 50½ Paulchoffatiidae; 51. Paurodontidae; 52. Pediomyidae; 53. Peradectidae?; 54. Peramuridae; 55. Peripitychidae; 56. Picopsidae; 57. Pinheirodontidae; 58. Plagiaulacidae; 59. Ptilodontidae; 60. Reigitheriidae; 61. Shuotheriidae; 62. Sinoconodontidae; 63. Sloanbaataridae; 64. Spalacotheriidae; 65. Stagodontidae; 66. Steropodontidae; 67. Sudamericidae; 68. Taeniolabididae; 69. Thereuodontidae; 70. Theroteinidae; 71. Tinodontidae; 72. Triconodontidae; 73. Vincelestidae; 74. Zalambdalestidae; 75. Zhelestidae; 76. Zofiabaataridae.

Another questionable record is a jaw fragment with three teeth, *Reigitherium*, from the Late Cretaceous Los Alamos Formation of Argentina that was regarded in its original description as a docodont (BONAPARTE, 1990) but is now regarded as *Mammalia incertae sedis* (KIELAN-JAWOROWSKA *et al.*, 2004).

Reflecting the fact that Mesozoic mammal sites are much more abundant in Laurasia, the eutriconodonts are much more frequent and diverse in Asia, Europe, and North America than in South America and Africa, the two Gondwana land masses with any record at all of this group. There are questionable records in the Early Jurassic of North America and India. By the Middle Jurassic, the eutriconodonts are well established in Asia and in the Late Jurassic, they occur in North America, Asia, and Africa. They are most widespread in the Early Cretaceous and persist into the Late Cretaceous in North and possibly South America. In Laurasia, there is enough of a record to at least suggest that some families were not present over that entire land mass. For example, while the Amphilestidae are

known from North America and Asia including India, the Triconodontidae are known only from North America and Europe, and the Gobiconodontidae are known only from Asia and North America.

The Haramiyida are first known and most widely known in the Late Triassic of Europe. Subsequently, there are records from single sites in the Early Jurassic of North America and the Late Jurassic of Africa. On the sparse evidence that exists, the group would seem to have dispersed from Europe to North America and Africa.

The most diverse group of Mesozoic mammals are the Multituberculata. Eighteen families are recognised of which only four occur on more than one continent, all in Laurasia. This pattern is quite different from their modern analogues, the rodents, which are much more widely spread. Of the 19 Recent rodent families, 13 have records on two or more continents. Although there are records of multituberculates on two of Gondwana continents, Africa and South America, these are based on few specimens whereas in Laurasia their remains are

common and taxonomically diverse.

Although not a highly diverse group, the “Symmetrodonts” are one of the most widespread of Mesozoic mammals between the Late Triassic and mid Cretaceous. This situation persisted from the time of Pangea in the Late Triassic to when the continents had split into Gondwana and Laurasia and those land masses in turn had begun to split apart by the mid Cretaceous. Five of the eight symmetrodont families are known from more than one continent. Two of the three that are restricted to one continent are known from the Late Cretaceous Los Alamos fauna of Patagonia. They may have survived as long as they did in South America because of the isolation of that continent. The Spalacotheriidae, in contrast to these restricted families, are known from Africa, Asia, Europe, South America, and North America in the Early to mid Cretaceous.

Monotremes are now known from the Cretaceous and Cainozoic of Australia, the Cainozoic of New Guinea, and the Early Cainozoic of South America. The only evidence to support the hypothesis that they originated in Australia is the fact that they are unknown in the Campanian Los Alamos local fauna of Patagonia. That this diverse mammalian assemblage does not include a monotreme implies that they had not yet reached South America at a time when they had been in Australia for at least 30 million years. Given that monotremes are generally regarded as quite primitive mammals and hence presumably a distinct lineage that came into existence in the early Mesozoic (RICH *et al.*, 2005), it is odd that they occur nowhere else in light of the configuration of the continents. However, given the meagre nature of the record of Jurassic fossil terrestrial vertebrates in Australia (one temnospondyl and one sauropod), monotremes quite likely thrived there through that period and are simply unknown and quite probably never will be.

Three of the eight families of eupantotheres are widespread geographically and have more than one genus in them. The other five have a single genus and are restricted to one continent. In addition to these, there are two African taxa which are not assigned to a genus and a number of European specimens that cannot be assigned to a genus or species, much less a family. Eupantotheres are most diverse in the Late Jurassic to Early Cretaceous. They occur on all the landmasses of Laurasia together with South America. The two South American families and species occur in the

Late Cretaceous Alamos fauna.

The oldest marsupials are in Laurasia, *Sinodelphis* from China being 125 myBP (LUO *et al.*, 2003) and *Kokopellia* from North America being 100 myBP (CIFELLI & MUIZON, 1997). As the diverse Los Alamos local fauna of Patagonia has a variety of archaic mammals more like those of the Jurassic elsewhere and lacks therians of any kind (BONAPARTE, 1990) while the early Palaeocene Tiupampa of Bolivia has both marsupials and placentals (MARSHALL *et al.*, 1995), this supports the conventional idea that marsupials arose in Laurasia and spread to South America. From South America, they reached Antarctica no later than the Eocene (WOODBURNE & ZINSMEISTER, 1982) and finally entered Australia in the Palaeocene or Eocene (GODTHELP *et al.*, 1992, 1999). What is not clear is whether there was a single marsupial dispersal event between South America and Australia, or multiple ones. Extant marsupials can be divided quite sharply into the Ameridelphia and the Australodelphia. As the names imply, the former is found in the Americas and with one exception, the latter in Australasia. This division was first recognised on the basis of foot structure (SZALAY, 1982) and subsequently supported by molecular data (NILSSON *et al.*, 2004). The one exception is the microbiothere *Dromiciops* from Chile, which is clearly an australodelphian. As *Dromiciops* appears to have been derived within the australodelphians, either its ancestors returned to South America after the dasyuromorphs plus peramelamorphs on the one hand and diprotodontians on the other differentiated in Australia, or the differentiation of the australodelphians into those two major groups occurred in South America and they independently reached Australia.

Turning to the eutherians, their Mesozoic palaeobiogeography is currently the most uncertain, particularly with regard to the placentals, those eutherians placed in extant orders. There are basically two schools of thought. The first is the “classical” school based primarily on the fossil record. The second is the “molecular” school based primarily on the analysis of DNA sequences.

The classic school holds that the eutherians arose in Laurasia and subsequently dispersed to Gondwana. This accords well with the vast bulk of the known mammalian fossil record, the oldest eutherian being *Eomaia scansoria* (JI *et al.*, 2002). The view that despite its unevenness, the fossil record is adequate to accurately characterise these

events is defended by FOOTE *et al.* (1999), and ARCHIBALD & DEUTSCHMANN (2001). Using statistical arguments regarding the completeness of the fossil record, they see the appearance of the eutherians as having taken place in the Early Cretaceous of Laurasia. Likewise, they regard the placentals as having arisen close to the time of their appearance in the fossil record; *i.e.*, in the aftermath of the KT boundary probably owing to the ecological release caused by the demise of the dinosaurs.

The molecular school is epitomised by MURPHY *et al.* (2001). Based on analysis of the DNA structure of modern species, four major clades of placentals are recognised: Afrotheria (Africa), Xenarthra (South America), Laurasiatheria, and Euarchontoglires. Laurasiatheria and Euarchontoglires are combined into the Boreutheria (Laurasia) (MURPHY *et al.*, 2001). The Afrotheria separated from the Xenarthra about 110 million years ago, the same time that the separation of Africa and South America occurred with the incursion of the South Atlantic. From there, under this view, the Boreutheria, which constitute the bulk of the placentals, reached North America and spread from there to Europe and Asia. The molecular data have been interpreted to mean that the majority of the modern placental orders arose ten to forty million years before their fossils are found in the fossil record. This constrains the time of movement of these placental groups to the Late

Cretaceous when the Afrotheres gave rise to the Xenarthra which moved across the South Atlantic about 103 million years ago (MURPHY *et al.*, 2001), the Xenarthra gave rise to the Boreosphenidians after that when they moved into Laurasia.

In the view of the classic school, the major weakness of the molecular school is the calibration points used to determine the age in years of the separation of the various placental clades from one another and thus the age of the clades themselves. In the view of the molecular school, the major weakness of the classic school is the incompleteness of the fossil record.

In the past eight years, a few tribosphenic mammal specimens have been found in the Middle Jurassic and Early Cretaceous of Gondwana. If they are not only indeed tribosphenic mammals, but also eutherians, this does not accord with the classic school. The fossils in question include the Middle Jurassic *Ambondro* (FLYNN *et al.*, 1999) based on a single lower jaw fragment from Madagascar, Middle Jurassic *Asfaltomylos* (RAUHUT *et al.*, 2002) based on a single lower jaw fragment from Argentina, and the Early Cretaceous *Ausktribosphenos* (RICH *et al.*, 1997) and *Bishops* (RICH *et al.*, 2001) based on about twenty lower jaw fragments from Australia (Fig.9). These forms have been variously interpreted. On the basis of their apparent tribosphenic dental morphology and dental formula, they have been allocated to the eutherians (WOODBURNE *et al.*, 2003).

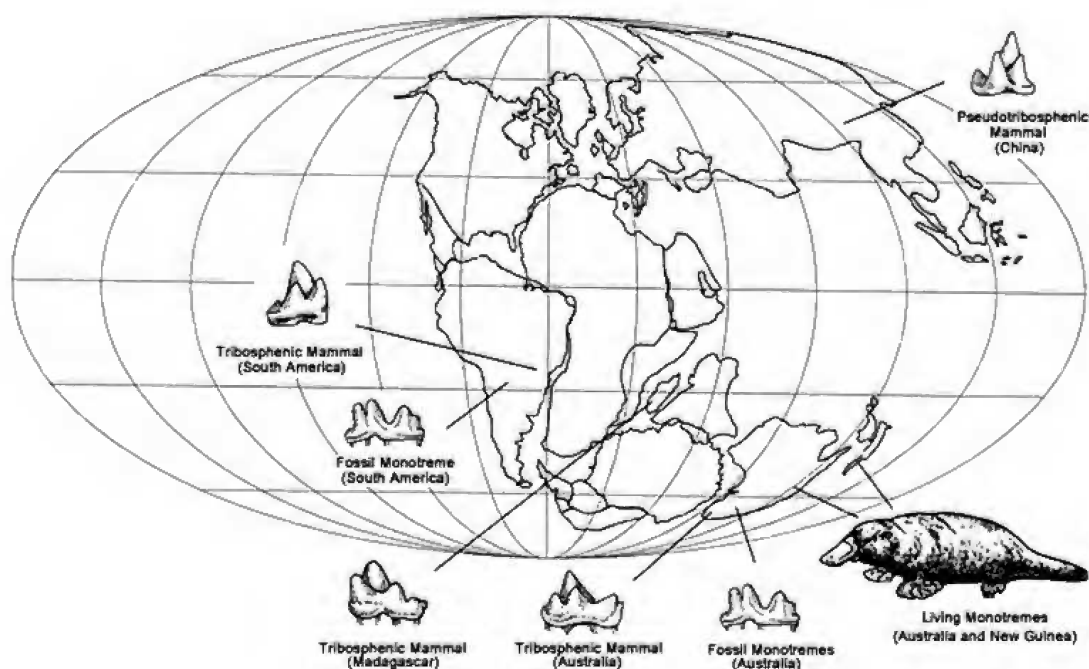


Fig.9- Geographic distribution of the Australosphenida of LUO *et al.* (2001). (Modified with permission from Zhe-Xi Luo. After Press Release of the Carnegie Museum of Natural History).

If this is the case, on the present evidence, eutherians arose earlier in Gondwana rather than in Laurasia. This accords with the idea based on molecular studies that placentals arose in Gondwana and subsequently spread to Laurasia. Alternatively, these forms have been united with the monotremes and the Middle Jurassic Chinese *Shuotherium* (CHOW & RICH, 1982), under the hypothesis that a separate radiation of mammals with a therian-like but not true tribosphenic dentition on a structurally primitive jaw took place in Gondwana (Fig.10) (LUO *et al.*, 2001, 2002). The primitive nature of the jaw was manifested in the presence of an internal mandibular groove. This group was dubbed the Australosphenida. The Laurasian eutherians were designated the Boreosphenida.

A cladogram of the Mammalia was constructed which grouped all of these australosphenidans together (Fig.11) (LUO *et al.*, 2001, 2002). Examination of the data matrix suggested that some important characters to this hypothesis could be interpreted quite differently (WOODBURNE *et al.*, 2003).

The essential aspects of the tribosphenic molar pattern are first that a cusp on the upper molar, the protocone acts as a mortar in a basin formed on the lower molar by the talonid. Second, that shearing occurs by successive upper molars abrading against the triangular pillar or trigonid of the lower molars, forming vertical or near vertical facets (Fig.12). The molars of the monotremes do not have the pattern of wear to be expected in a tribosphenic mammal (LUO *et al.*, 2002) (Fig.13, see especially D₂). There is no talonid on the lower molars into which a protocone occludes. Likewise, no near vertical wear facets are present. Most mammals in fact do not have a tribosphenic dentition although they are clearly descended from ancestors that did. It could very well be that monotremes are descended from an ancestor with a tribosphenic dentition. But if so, the modifications that the teeth have undergone are so great that there is no trace of them having had a tribosphenic ancestor. In any case, the morphology of these teeth does not add evidence allying the monotremes with the tribosphenic australodelphidans (RICH *et al.*, 2002).

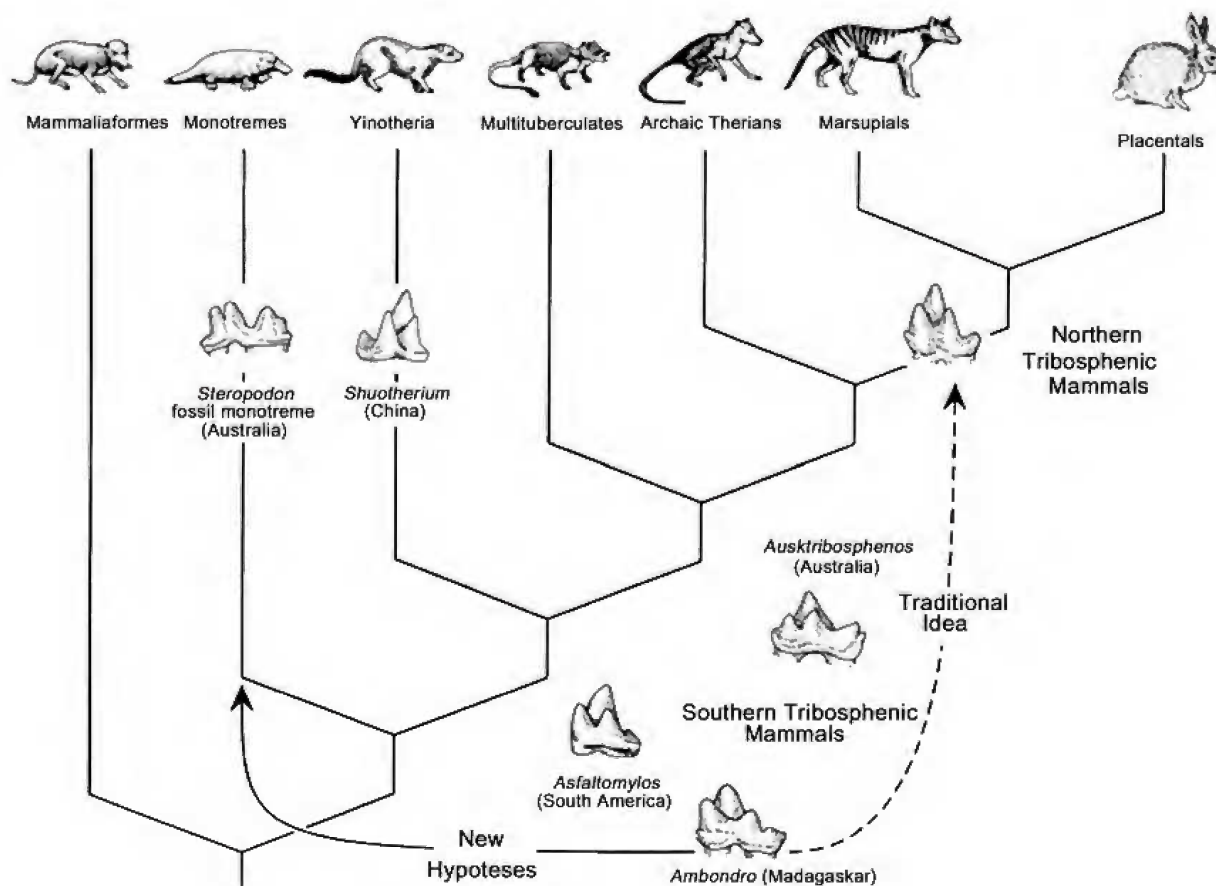


Fig.10- Alternative phylogenies of the tribosphenic members of the Australosphenida of Luo *et al.* (2001). (Modified with permission from Zhe-Xi Luo. After Press Release of the Carnegie Museum of Natural History).

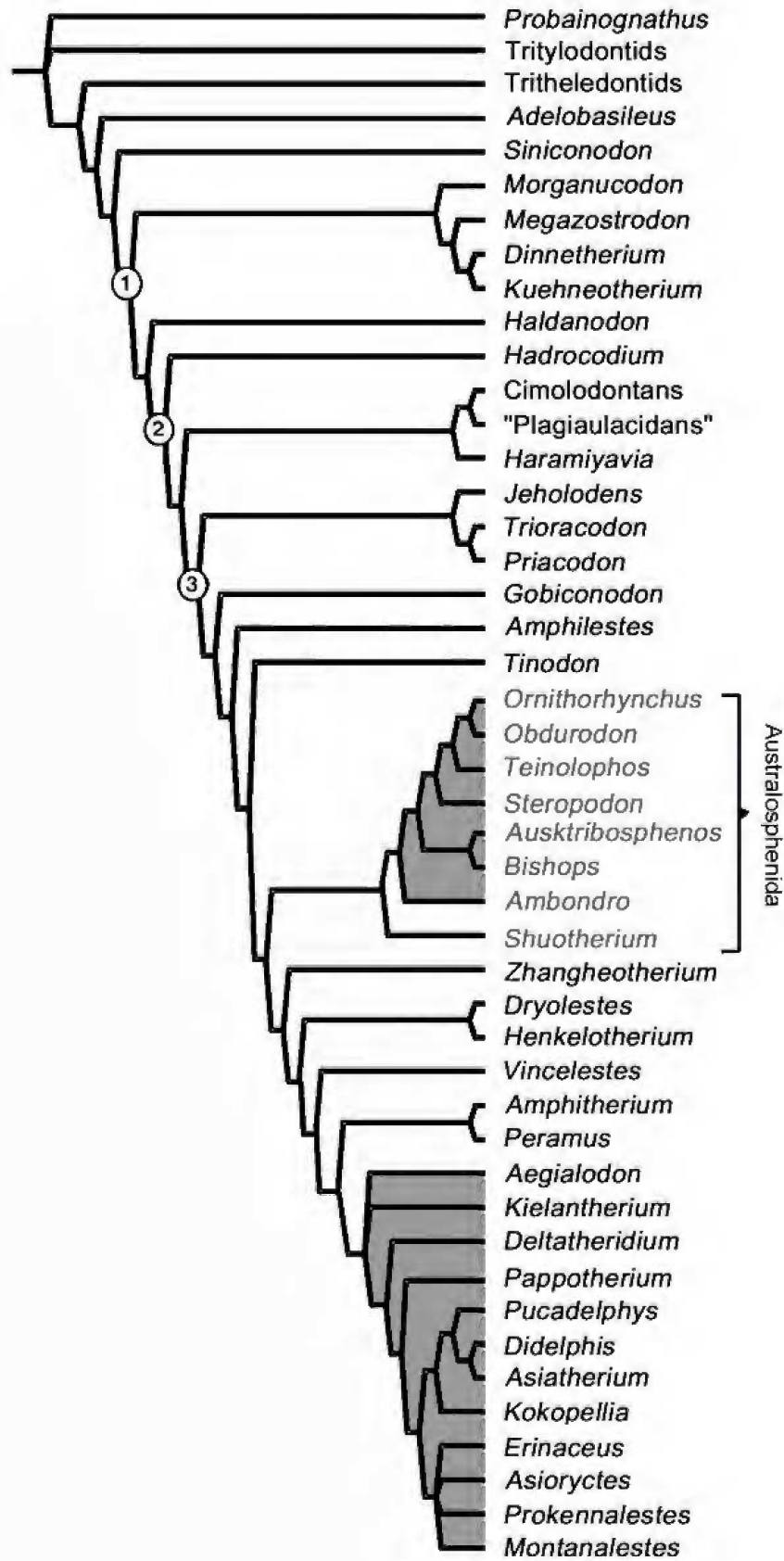


Fig. 11- Cladogram of the relationships of the Mammalia in Luo *et al.* (2002). Note that the members of the Australosphenida are all clustered together.

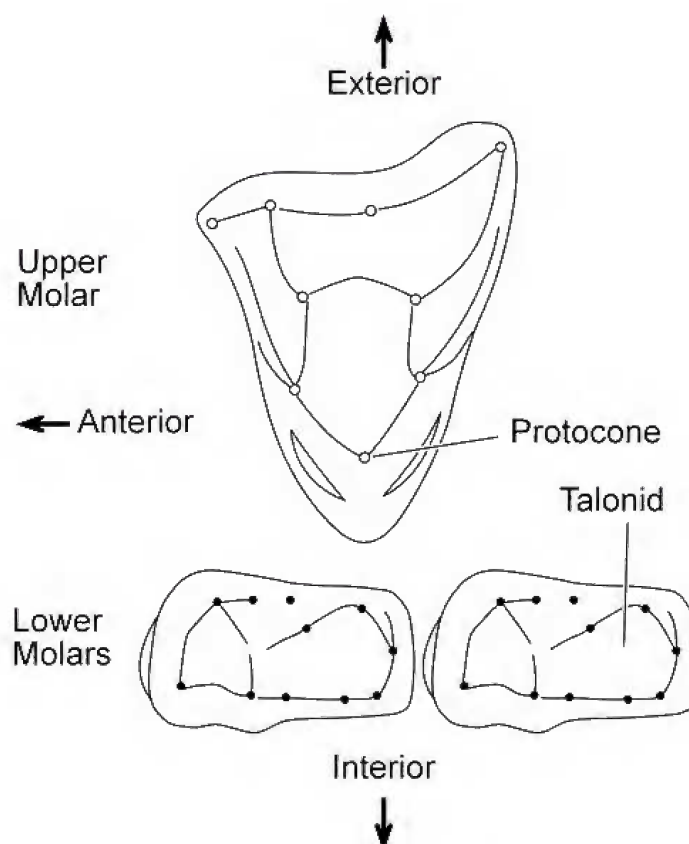


Fig.12- Diagrammatic tribosphenic upper and lower molars. Note that the protocone occludes in the talonid basin with a mortar and pestle action while the preprotocrista forms a vertical shearing surface in slicing past the posterior vertical side of the talonid basin and the postprotocrista forms a vertical shearing surface in slicing past the posterior side of the trigonid.

For that matter, the dental pattern of the monotremes is as close to the boreosphenidians as to the australosphenidians.

The australosphenidians are characterised as having an advanced tribosphenic dentition on a primitive mandible (LUO *et al.*, 2002). The primitive feature being a Meckelian groove. This character of the jaw is quite variable in the taxa regarded as australosphenidians. On the monotreme *Teinolophos* (Fig.14), the groove is quite deep while in the monotreme *Steropodon*, it is non-existent. In the ausktribosphenid *Austribosphenos* (Fig.15), there is a shallow groove while in the other known ausktribosphenid *Bishops* (Fig.16), there is no groove at all. The yinothere *Shuotherium* (Fig.17) has a shallow groove as does the unquestioned boreosphenidian *Prokennalestes* (KIELAN-JAWOROWSKA & DASHZEVEG, 1989) (Fig.18). Thus it seems that this feature of the jaw is not a consistent one within the australosphenidians. In any case, the presence of an internal mandibular groove is a plesiomorphic character and thus of little value in establishing relationships.

The australosphenidians and boreosphenidians have been separated on the basis of the height of the condyle and the orientation of the angle (Fig.19). Whilst this division holds in the specimens shown in the lefthand column of figure 19 (Fig.5 in LUO *et al.*, 2002) additional erinaceids shown in the righthand column (various figures in BUTLER, 1948) have the orientation of these structures similar to the australosphenidians and thus this character does not distinguish the australosphenidians from the boreosphenidians.

A cingulum wrapping around the paraconid of the australosphenidians is considered to be a principal feature of that group distinguishing it from the boreosphenidians (LUO *et al.*, 2002). Unfortunately, the view of the lower molar of *Teinolophos* shown in LUO *et al.* (2002) is lingual (Fig.20D) whereas all the other teeth in that figure are in labial view. The actual labial view is to the right of figure 20D.

When these character differences were incorporated into the data matrix of LUO *et al.* (2002), the tribosphenic australosphenidians clustered with the

eutherians whereas the monotremes and *Shuotherium* were quite remote from that group (Fig.21) (WOODBURNE *et al.*, 2003).

In light of this, it is tempting to conclude that the eutherians arose in Gondwana and subsequently spread to Laurasia. However, the Middle Jurassic when *Ambondro* and *Asfaltomylos* lived is extremely poorly known. So, on the basis of the fossils, Lillegraven's conclusion, "somewhere on the Earth's dry surface," is probably the most realistic conclusion to come to regarding the place of origin of the eutherians.

Molecular studies suggest that the majority of the living orders of placentals arose well before the KT boundary. This is in contrast to the fossil record which only identifies a few pre-Tertiary orders. If the molecular interpretation is correct and there are many extant placental orders which originated in the Late Cretaceous, it implies that there is a significant missing fossil record. If that is the case, it is likely to be in areas that until now have been poorly sampled. This is the Garden of Eden. Hypothesis of FOOTE *et al.* (1999).

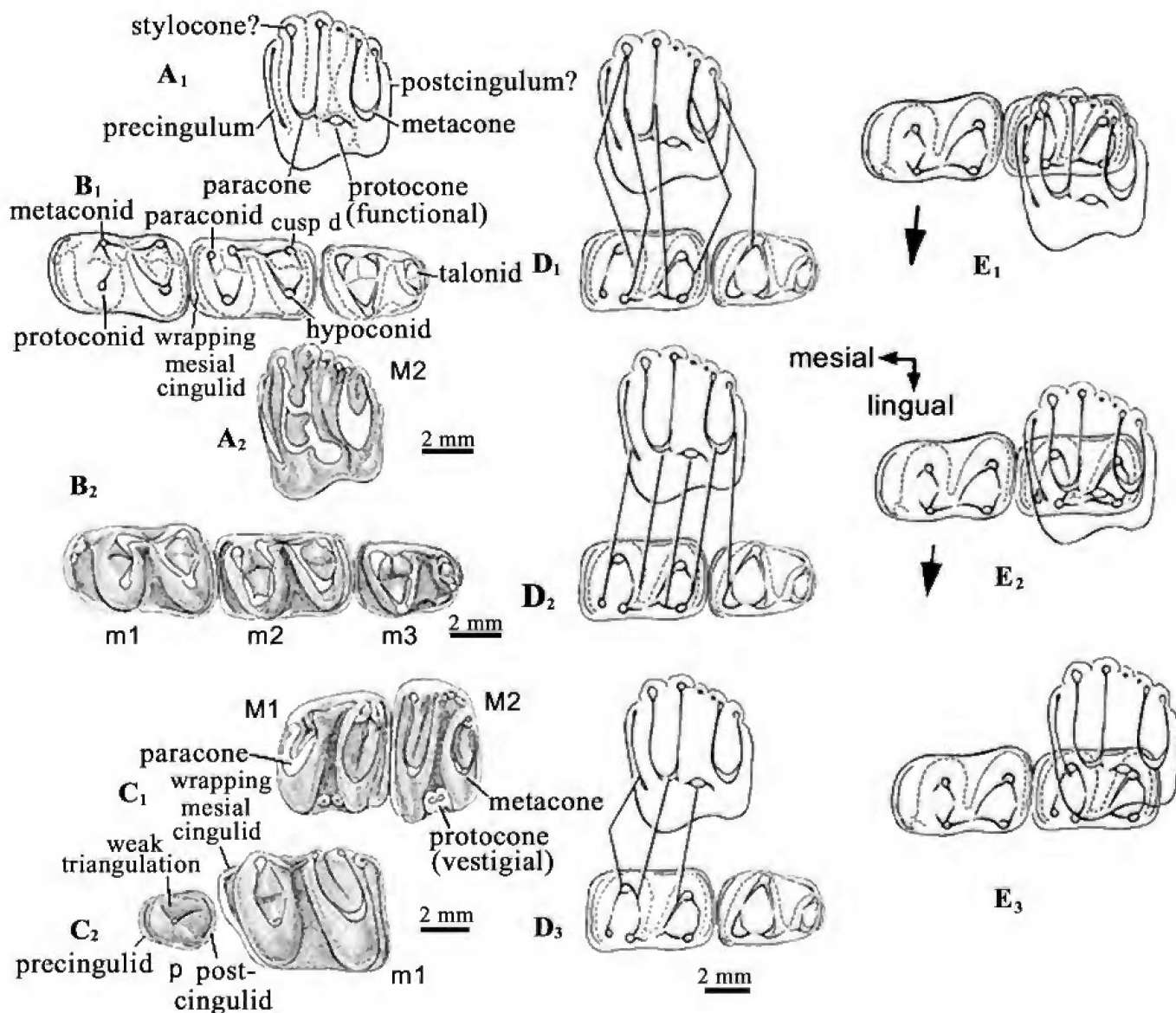


Fig.13- Diagrammatic monotreme occlusal patterns. A₁₋₂. Upper molar of *Monotrematum sudamericanum*. B₁₋₂. Lower molars of *Steropodon galmani*. C₁. Upper molars of *Obdurodon dicksoni*. C₂. Lower premolar and molar of *Obdurodon dicksoni*. D. Hypothetical occlusal relationships between upper and lower monotreme molars. D₁. Beginning of occlusal cycle. D₂. Middle of occlusal cycle which shows a functional protocone that is interpreted as having had a mortar and pestle action against cusp d. Even if this occlusal relationship did exist, it is analogous, not homologous to the tribosphenic pattern. D₃. End of occlusal cycle. E₁₋₃. Superimposed relationship of upper and lower monotreme molars, each numerical stage corresponding to the equivalent number in D₁₋₃. After LUO *et al.* (2002).

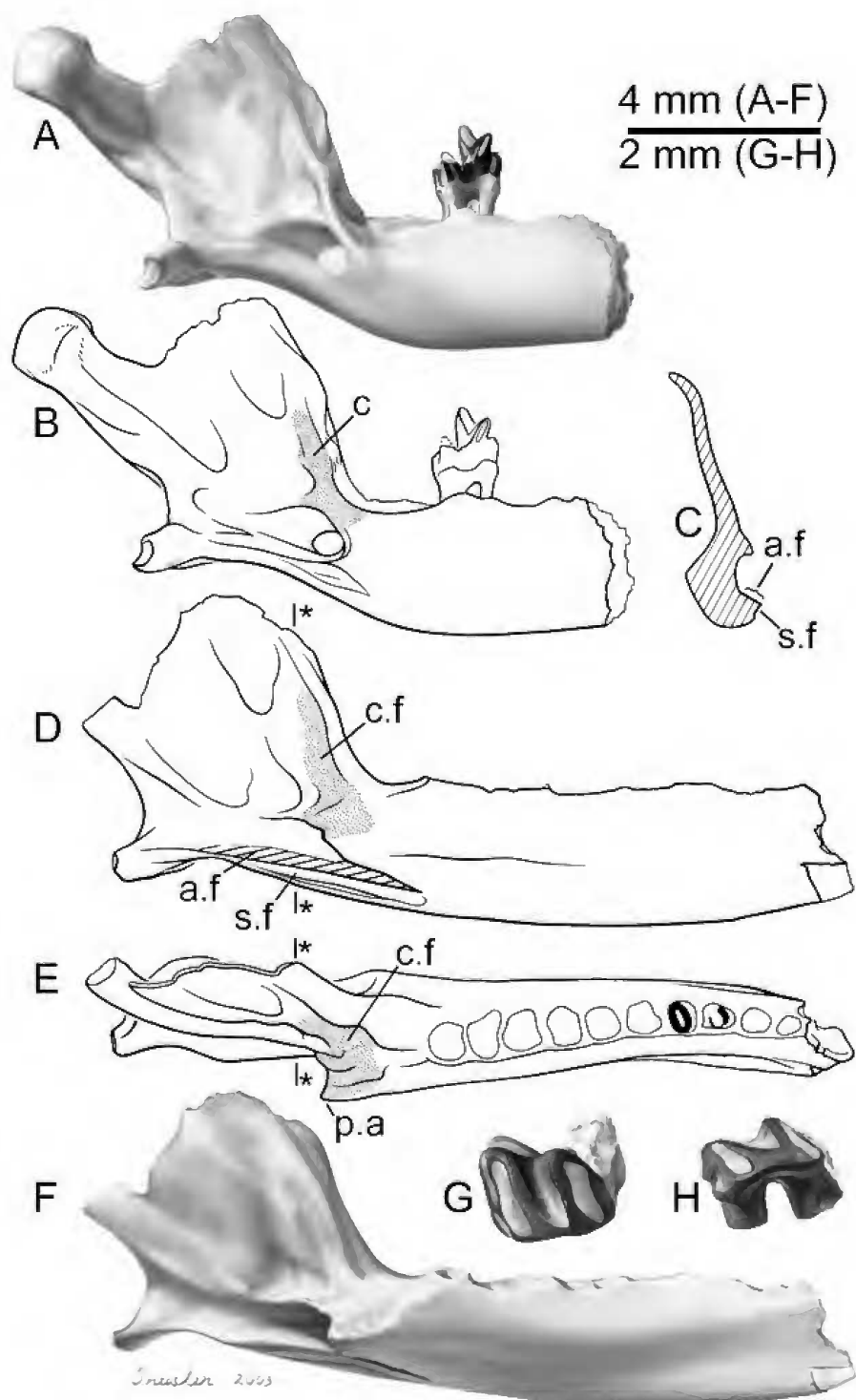


Fig.14- A. Medial view of holotype of *Teinolophos trusleri*, NMV P208231. B. Diagrammatic medial view of NMV P208231; the stippled area indicates the position of the fused coronoid bone. C. Cross section of mandible of referred specimen of *T. trusleri*, NMV P212933; position of cross section indicated in figures 14D and 14E, by lines terminated with stars. D. Diagrammatic medial view of NMV P212933. The stippled area indicates the position of the contact facet for the coronoid bone. Traces of roots of a molar can be seen in alveoli three and four. E. Diagrammatic dorsal view of NMV P212933. Traces of roots of a molar can be seen in alveoli three and four. F. Medial view of NMV P212933, rotated slightly medially towards the viewer. G. Occlusal and (H) medial views of isolated lower molar associated with dentary, NMV P212933. Abbreviations: a.f, angular facet; a.p, angular process; c, coronoid; c.f, coronoid facet; m.f, mandibular foramen; m.t, mandibular trough; p.a, posterointernal angle; s.f, splenial facet. (From RICH *et al.*, 2005).

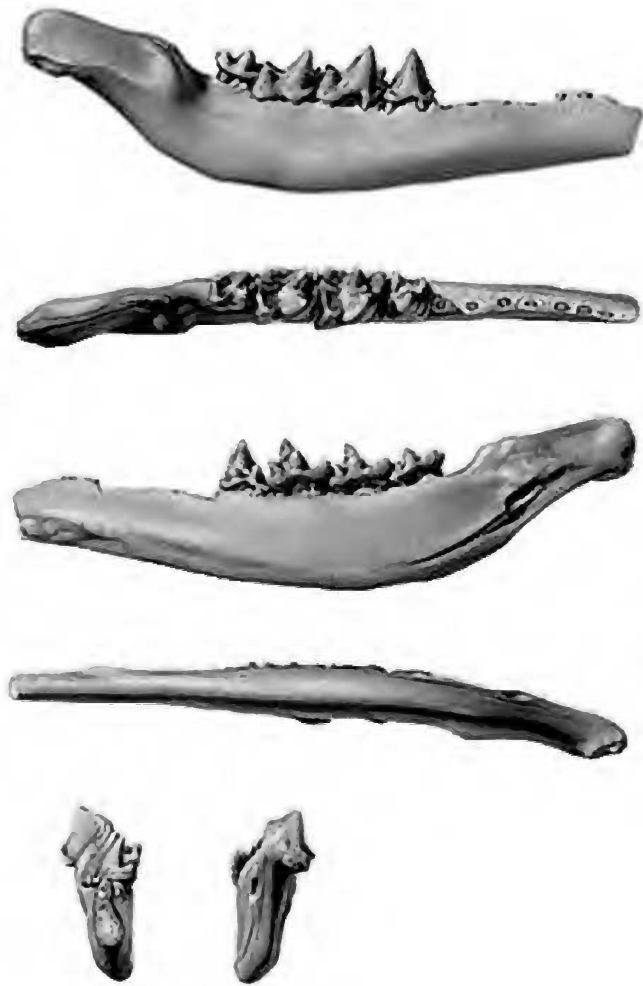


Fig.15- Right mandible of the tribosphenic mammal *Ausktribosphenos nyktos* Rich, Vickers-Rich, Constantine, Flannery, Kool & Van Klaveren, 1997 (Fig.2). From the Aptian Strzelecki Group, Flat Rocks, Victoria, Australia.

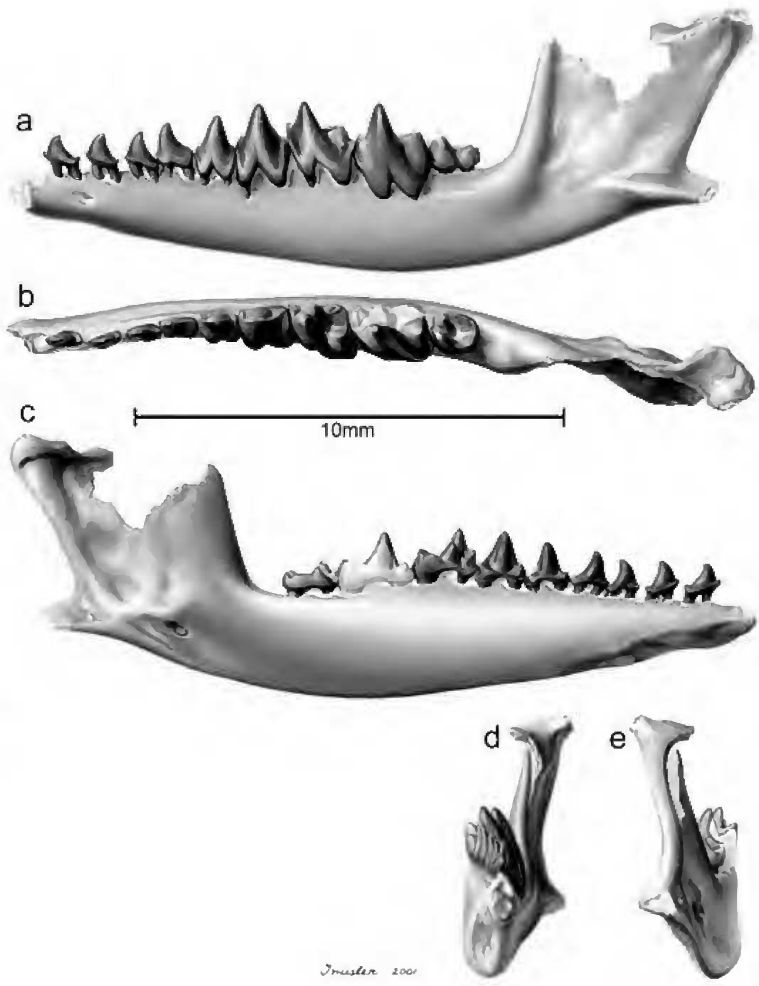


Fig.16- Left mandible of the tribosphenic mammal *Bishops whitmorei* Rich, Flannery, Trusler, Kool, Van Klaveren & Vickers-Rich, 2001 (Fig.1). From the Aptian Strzelecki Group, Flat Rocks, Victoria, Australia.



Fig.17- Left mandible of the yinothere *Shuotherium dongi* Chow & Rich, 1982 (Fig.5B).

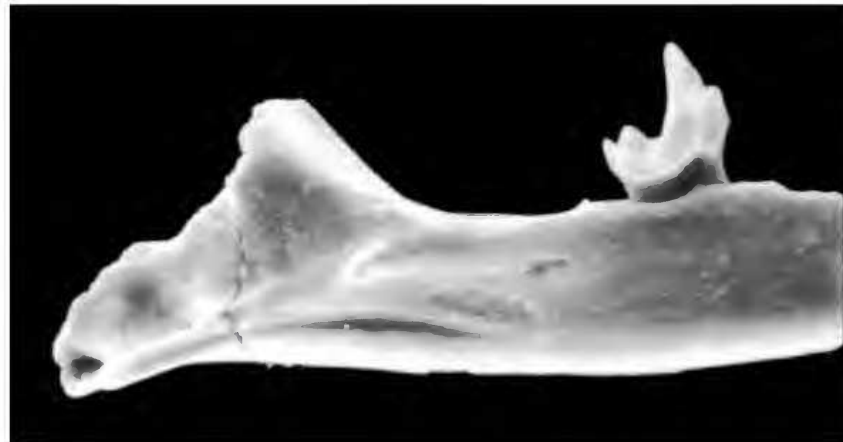


Fig.18- Left mandible of the placental *Prokennalestes minor* Kielan-Jaworowska & Dashzeveg, 1989 (Fig.23).

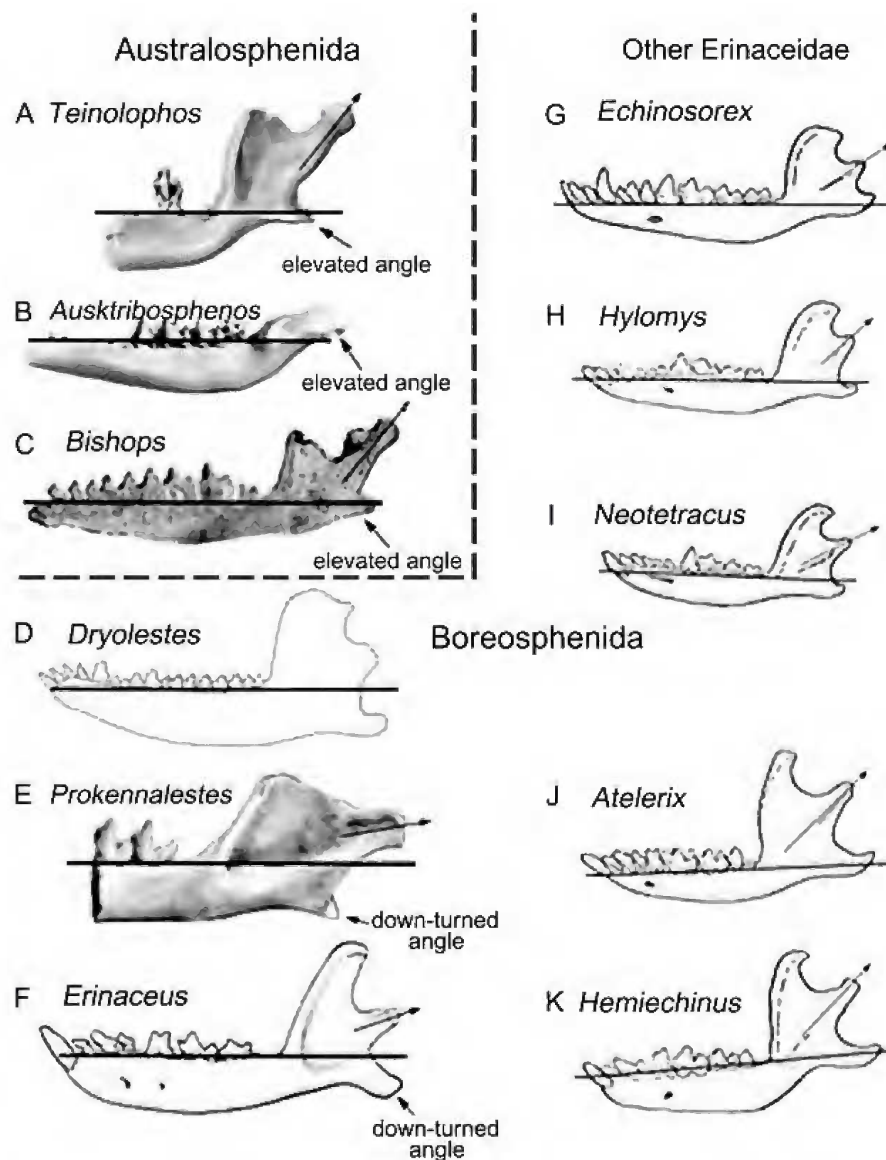


Fig.19- Comparison of the height of the condyle and orientation of the condyle on the mandible of boreosphenidians and australosphenidians. See text for discussion. From BUTLER (1948) and LUO *et al.* (2002).

FOOTE *et al.* (1999) and ARCHIBALD & DEUTSCHMANN (2001) both present actuarial arguments that the fossil record should be taken as given. That is, it is reliable enough to accept the dates of first appearance of groups as close to their dates of origin. Where this approach is weak in this instance is evaluating the record of land masses with no Late Cretaceous mammal sites; *i.e.*, Antarctica, Africa, and Australia.

HUNTER & JANIS (2006) put forward a hypothesis asserting that the placentals arose in the Northern Hemisphere. This was based in part on two parsimony arguments. The first was minimization of the amount of missing evolutionary history

(FOOTE *et al.*, 1999). While this may be the best procedure to handle the data available, whether, given the uneven record of fossil placentals on various continents, it is even close enough to the actual events to be a useful guide rather than misleading is not clear. Second, it is not certain that a model which has the fewest number of continental interchanges for the various placental mammalian orders is the best estimate of their places of origin. In this instance, parsimony is regarded as a trustworthy guide for deciding between one geographic model and another because intercontinental interchanges are considered unlikely (MCKENNA, 1973).

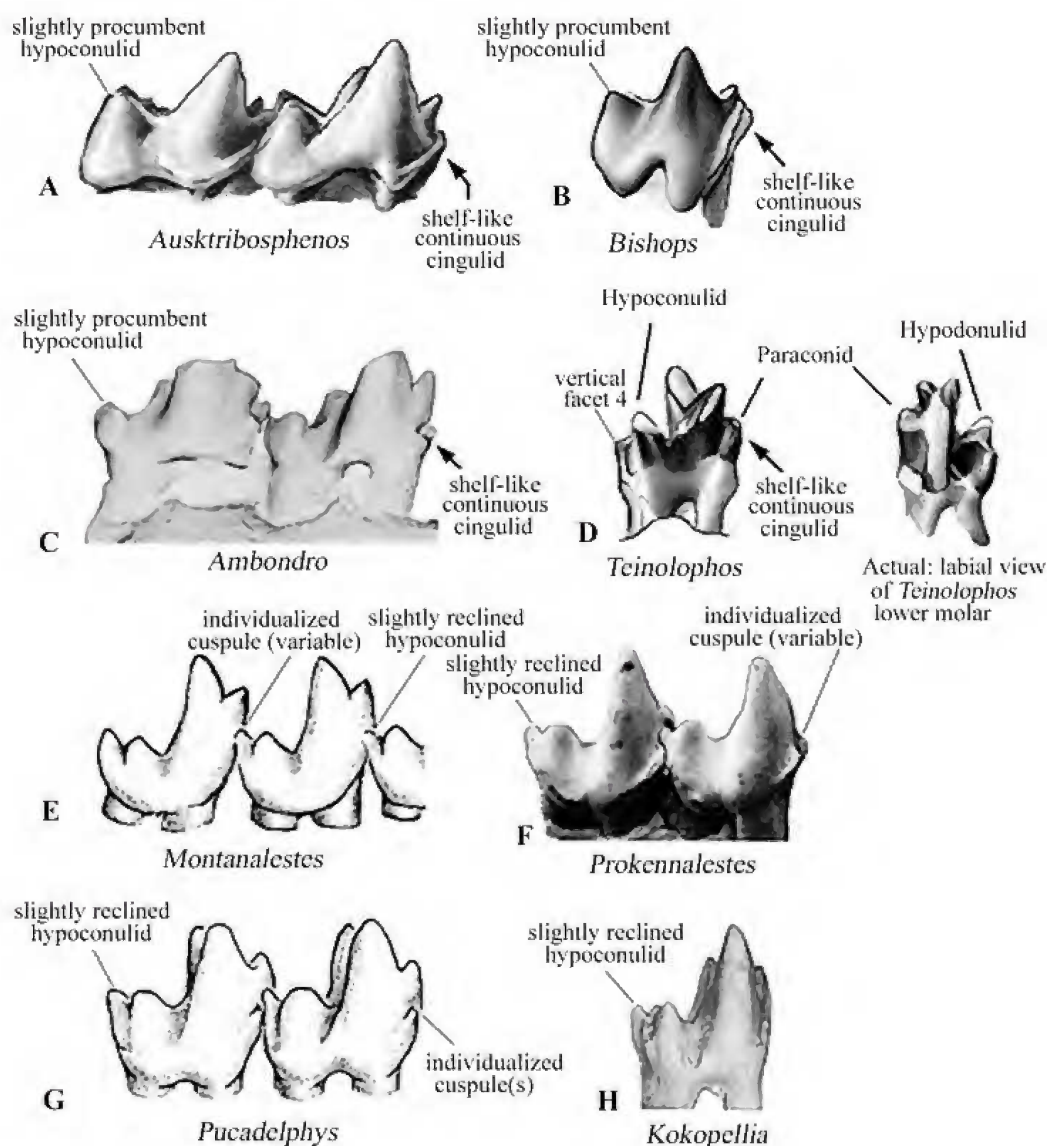


Fig.20- Comparison of the dentitions of australosphenidians and boreosphenidians. See text for discussion. From Luo *et al.* (2002).

However, such interchanges are not always rare. For example, between North and South America in the Pliocene Great American Interchange, 46 different genera individually passed from one continent to the other (WEBB, 1985). This is far more than the ordinal interchanges analysed by HUNTER & JANIS (2006). If exchanges are possible at all does their number provide a meaningful measure of the likelihood? Given the smaller numbers in the models compared by HUNTER & JANIS (2006), one can only wonder at just how meaningful

the significance of the numerical differences is.

CONCLUSIONS

Knowledge of the palaeobiogeography of Mesozoic mammals is extremely meagre and uneven both in time and space. Reconciliation of the interpretations of the fossil and molecular evidence relating to this problem is as central to future progress about this question as the discovery of additional fossils.

Woodburne et al. (2003) Fig. 2

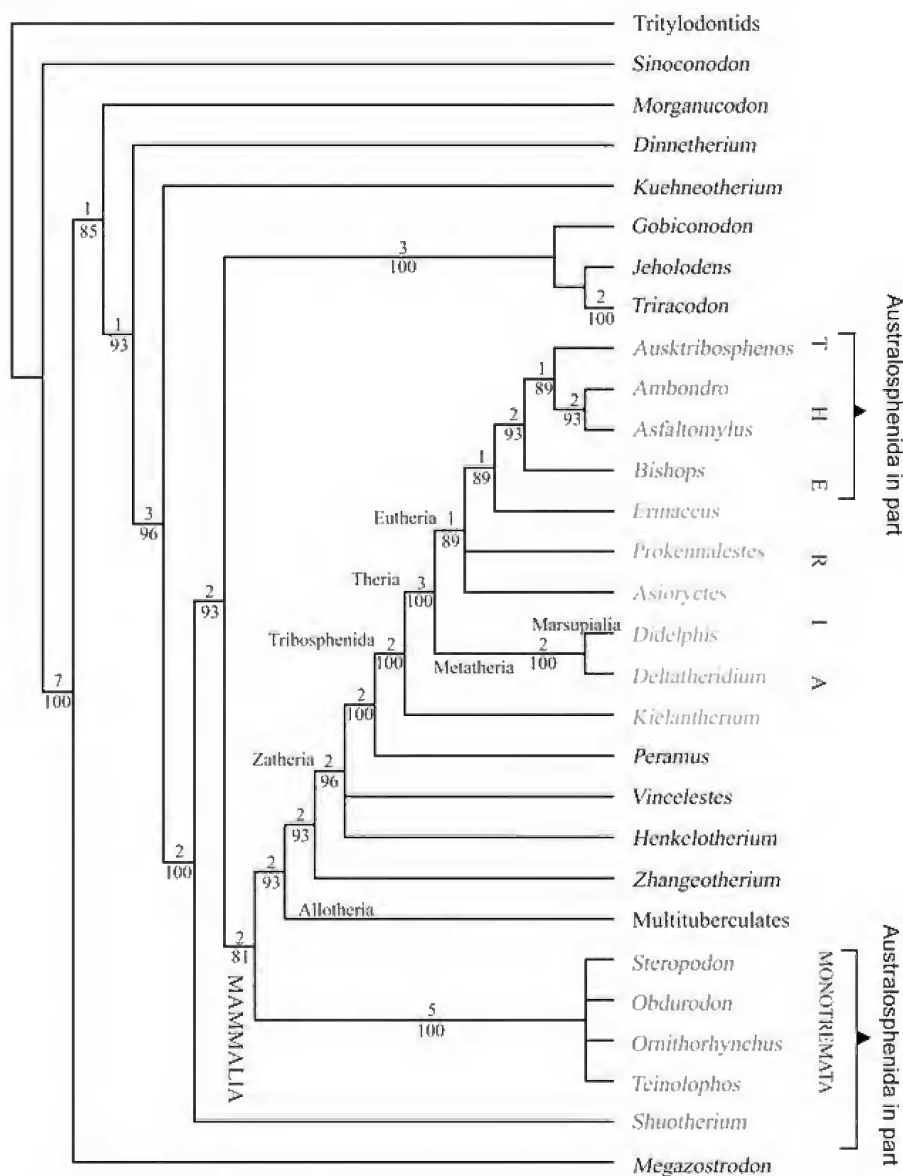


Fig.21- Alternative cladogram of the relationships of the Mammalia (Fig.2 in WOODBURNE et al., 2003). The characters analysed in this cladogram were virtually the same as those in figure 11. That the cladograms are not the same is owing to differences in the assignment of character states. Whereas the australosphenidians were recognized by LUO et al. (2002) as a single entity, they are divided into the three groups indicated here: (1) eutherians?, (2) monotremes, and (3) *Shuotherium* (yinothere).

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This contribution is dedicated to the memory of Malcolm Carnegie McKenna (21 July 1930 - 3 March 2008), generous and inspiring mentor to numerous students and renowned palaeomammalogist.

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